

SHORT DISTANCE FORM FREQUENCY DIFFERENCES IN MELANIC LEPIDOPTERA ACROSS HABITAT BOUNDARIES

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The evolution of industrial melanism in the peppered moth, *Biston betularia* (L.), is considered to be a classic example of evolution in action. The primary selective agent involved has been shown to be differential bird predation, the melanic morph *f. carbonaria* being more cryptic in heavily polluted regions, but less cryptic than the typical form in relatively unpolluted areas (Kettlewell, 1955a, 1956). Mani (1990) has successfully shown by computer simulation that fitness differences between the forms estimated from bird predation experiments provide good agreement with geographic differences in the frequencies of the forms, at least on a coarse scale.

Recent work on melanic polymorphism in other species of Lepidoptera has shown that the frequencies of melanic forms may change abruptly and significantly over very short distances across habitat boundaries. Kearns and Majerus (1987) showed that the frequencies of melanic forms of *Alcis repandata* (L.) and *Semiothisa liturata* (Clerck), taken in a moth trap under a close plantation conifer canopy, in Dyfed, Wales, were significantly higher than in a moth trap some 50 yards away in open deciduous woodland. Similar results have subsequently been obtained for *Agriopis marginaria* (F.) (Majerus, 1989) in Hampshire, *A. repandata*, *Peribatodes rhomboidaria* (D. & S.) and *Idaea aversata* (L.), in Surrey (Jones *et al.*, in press), and *Chloroclysta truncata* (Hufn.), *Thera obeliscata* (Hübner), *Thera firmata* (Hübner) and *Noctua pronuba* L., in Gloucestershire (Aldridge *et al.*, 1993).

We here provide data from a short period of moth trapping at Box Hill, Surrey showing that morph specific frequency differences over short distances occur in many, but not all, species of moth with melanic forms. In so doing we extend the list of species in which significant habitat-related frequency differences have been recorded, and provide the first data showing species in which such differences do not occur.

METHODS

Trapping was carried out from 22.vi to 2.vii.1992, between approximately 21.30 p.m. and 1.00 a.m., in Juniper Bottom, Box Hill, Surrey.

Juniper Bottom is an east-west running valley with mature yew woodland along its sides. The canopy of the wood is extremely dense leading to a very dark under-canopy with virtually no ground cover, except under occasional broad-leaf trees, such as whitebeam, and below breaks in the canopy caused by the blowdowns of October 1987. This sparse ground cover consists mainly of dog's mercury.

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The bottom of the valley is separated from the yew slopes by a sharply defined, thick, mixed broad-leaf natural hedge. This provides a sharp habitat boundary between the darkness inside the wood and the light of the open valley floor. The valley floor is characterized by short, partly rabbit-cropped, chalk grassland. (For further details of the vegetation types see Jones *et al.*, 1993.)

The traps used were 100-W mercury vapour discharge bulbs set on 'dustbin' traps. They were set in pairs across the habitat boundary approximately 27 m apart and with 77 m between each pair.

Nine species with melanic forms were scored as typical, half-melanic, melanic or dark banded according to morph phenotype. For *Apamea monoglypha* (Hufn.), which displayed continuous variation, the morphs were graded from 1 to 5, lightest to darkest respectively, using representative standard individuals of each class for comparison. Similarly, for *Hydriomena furcata* (Thunb.), many different morphs were seen. They were recorded according to colour (yellow, green or pink), pattern (speckled or banded), strength of pattern and whether they were melanic, half-melanic or typical (absence of large areas of black). For statistical analysis only melanic, half melanic and typical classes were considered. The numbers of three species, *N. pronuba*, *Craniophora ligustri* (D. & S.) and *B. betularia* were too small for any meaningful analysis to be performed or deductions to be drawn, and results for these three are not included.

RESULTS AND ANALYSIS

The results for six species are given in Table 1. The data were analysed using heterogeneity chi-squared analysis. (The chi-squared test determines the probability

Table 1. The numbers of moths of different forms of six species taken in yew woodland or in chalk grassland at Juniper Bottom from 22.vi to 2.vii.1992. Data from the three traps set each night in the yew woodland are totalled. Similarly the data from the three traps set in chalk grassland each night are totalled.

<i>Peribatodes rhomboidaria</i>	Typical		Melanic		Total	
Yew woodland	85		66		151	
Chalk grassland	46		8		54	
<i>Alcis repandata</i>	Typical	Half-melanic	Melanic	Banded	Total	
Yew woodland	47	97	16	13	173	
Chalk grassland	43	39	11	5	98	
<i>Ectropis bistortata</i>	Typical	Half-melanic	Melanic		Total	
Yew woodland	17	5	6		28	
Chalk grassland	35	2	5		42	
<i>Idaea aversata</i>	Unbanded		Banded		Total	
Yew woodland	34		13		47	
Chalk grassland	17		3		20	
<i>Apamea monoglypha</i>	Darkest	←	Class	→	Lightest	
	5	4	3	2	1	Total
Yew woodland	1	0	10	4	2	17
Chalk grassland	2	2	13	9	0	26
<i>Hydriomena furcata</i>	Typical	Half-melanic	Melanic		Total	
Yew woodland	22	5	25		52	
Chalk grassland	27	8	18		53	

that a particular deviation, in an observed data set, from the expectation based on a scientific hypothesis, for example that the frequencies of typical and melanic *P. rhomboidaria* should be the same in yew woodland and chalk grassland, could occur by chance sampling error.) The comparisons tested, the chi-squared values, degrees of freedom and corresponding probabilities are given in Table 2.

The data from *P. rhomboidaria* and *A. repandata* confirm the findings of Jones *et al.* (1993). In *P. rhomboidaria*, significantly more melanics were taken under the yew canopy than in the chalk grassland. (In this context, significant is used as a technical statistical term, meaning that the likelihood that a particular deviation from expectation is less than one in twenty, if the usual significant level (P) of 0.05 is set.) In *A. repandata*, the relative frequencies of the half-melanic, melanic and banded forms were homogeneous in the two habitats, with the frequencies of all three being higher under the yew canopy than in chalk grassland. However, the frequency of the typical form when compared to the three darker morphs was significantly higher in the chalk grassland than under the yew canopy.

In the case of *I. aversata*, the frequency of the banded form was higher in the yew traps than in the chalk grassland traps, but not significantly so. However, the data are not significantly different from those obtained by Jones *et al.* (1993), when trapping at Juniper Bottom, in 1990 (data given in Table 3 for convenience) either under the yew ($\chi^2_1 = 0.070$; $P > 0.05$), or in the chalk grassland ($\chi^2_1 = 0.700$; $P > 0.05$).

The frequencies of darker forms (half-melanic and melanic) of *Ectropis bistortata* (Goeze) were significantly higher inside the yew woodland than in the chalk grassland.

Conversely, the frequencies of the darker grades (classes 3, 4 and 5) of *A. monoglypha*, did not differ significantly from those of the paler grades in the two habitats. In *H. furcata*, the frequency of full melanics in the yew traps was

Table 2. Analysis of data, giving chi-squared (χ^2) values, degrees of freedom (d.f.) and probabilities (P) (ns = non-significant).

	χ^2	d.f.	P
<i>P. rhomboidaria</i>			
Typical vs melanic, yew vs grass:	14.40	1	<0.001
<i>A. repandata</i>			
All forms, yew vs grass:	9.352	3	<0.05
Melanic vs half-melanic, yew vs grass:	1.610	1	ns
Melanic + half-melanic vs banded, yew vs grass:	0.064	1	ns
Melanic + half-melanic + banded vs typical, yew vs grass:	7.869	1	<0.05
<i>E. bistortata</i>			
Melanic + half-melanic vs typical, yew vs grass:	4.500	1	<0.05
<i>I. aversata</i>			
Typical vs banded, yew vs grass:	1.237	1	ns
<i>A. monoglypha</i>			
Classes 1 + 2 vs classes 3 + 4 + 5, yew vs grass:	0.002	1	ns
<i>H. furcata</i>			
Typical + half-melanic vs melanic, yew vs grass:	2.157	1	ns

Table 3. Numbers of two forms of *I. aversata* taken in paired m.v. light traps at Juniper Bottom, Box Hill, Surrey, 22.vi–6.vii.1990. Traps of a pair were sited 20 m apart, one inside and one outside mature yew woodland. (From Jones *et al.*, 1993.)

	Unbanded	Banded	Total
Inside yew	51	27	78
Outside yew	23	3	26

The banded form is the nominate form. The unbanded form is *f. remutata*.

Test of unbanded vs banded, inside vs outside yew woodland: $\chi^2_1 = 5.05$, $P < 0.05$.

higher than in the chalk grassland, the converse being the case for both the typical and half-melanic classes, but the differences were very slight.

DISCUSSION

Jones *et al.* (1993) suggested two possible causes for the presence of higher frequencies of melanic and dark banded forms under dark canopies than in more open habitats. Either, as a result of selective predation by birds in the past, morph-specific habitat preferences have evolved so that their degree of crypsis and thus protection from visually hunting predators is maximized. Alternatively, in the absence of such preferences, continual bird predation, by eliminating light forms in dark habitats, and dark forms in open habitats, may maintain the frequency differences year on year. Several authors make the assertion that the latter is an unlikely explanation because the level of differential bird predation would have to be very high to maintain abrupt frequency differences over such short distances (Majerus, 1989; Jones *et al.*, 1993; Aldridge *et al.*, 1993). However, Jones (1993) has shown that sharp clines in morph frequencies may be maintained by relatively weak differential bird predation, as long as dispersal distances are not high.

Aldridge *et al.* (1993) put forward a third hypothesis, namely that differential habitat selection has evolved for reasons not associated with bird predation and the degree of crypsis. They note, as a possibility, that the night temperature would generally be higher under closed woodland canopies than in the open. As the degree of irradiation from a surface is at least in part dependent on its colour, a dark surface radiating heat faster than a pale one, they suggest that melanics may be at a disadvantage if they fly in cooler more open situations. However, in this context it must also be pertinent to ask why some species appear not to show morph-related habitat selection.

While the data available are not sufficient to allow more than speculation on the three alternative explanations of the data, consideration of the origin and genetic control of melanism in the species which do, and those which do not show abrupt frequency differences, may be informative. In all the species in which sharp morph frequency differences over short distances have been recorded previously, the melanism is thought to be controlled by one or two genetic loci, and to be of relatively ancient origin (Jones *et al.*, 1993; Aldridge *et al.*, 1993). This is significant because Howlett (1989) has demonstrated that morph-specific behavioural differences will take substantial amounts of time to evolve. The likelihood of morph-specific habitat preferences evolving will thus increase with time, and be more frequent in species in which melanism is of relatively ancient origin.

In *E. bistortata*, Kettlewell (1973) cites melanism as being '? industrial', from a number of sites in southern England and Wales. The inheritance of melanism

is not noted, but progeny from a number of crosses suggest that half-melanism and melanics are controlled by separate single loci, with their respective alleles both dominant to the typical alleles (Majerus, unpublished). Jones (1993) questions Kettlewell's suggestion that melanism in *E. bistrorata* is industrial in origin, noting the occurrence of melanic individuals from a number of rural regions.

In both *A. monoglypha* and *H. furcata*, Kettlewell (1973) reports the existence of ancient, non-industrial melanics. In neither species has the inheritance of the colour pattern variation been analysed, but the continuous variation in *A. monoglypha* is likely to be under polygenic control, with the darkest form, f. *aethiops* Tutt (not present in the Juniper Bottom samples), possibly being due to a single gene showing incomplete dominance (Kettlewell, 1973). In *H. furcata* preliminary analysis suggests at least five gene loci are involved, three of these respectively controlling ground colour, flecking, banding, and two affecting melanism (Majerus, unpublished data). That the genetic control of melanism in the two species which do not show sharp morph-specific frequency changes is more complex than that in any of the species which do show this phenomenon, raises the possibility that the mode of inheritance of melanism, as well as its time origin, may be important in the evolution of morph-specific habitat preferences. If the mechanism by which a particular type of behaviour (such as actively preferring a particular habitat) becomes associated with a specific phenotype is because the genes controlling the behaviour and the phenotype are tightly linked, as suggested by Howlett (1989), such linkage may only be possible if melanism is controlled by one or two gene loci. In species where melanism is controlled polygenically, it may be that morph-specific habitat preferences and morph-specific resting site preferences can only evolve if choice is made through a mechanism such as Kettlewell's (1955b) contrast-conflict hypothesis of resting site selection. That is to say if a moth's behaviour is dependent on its own perception of its phenotype.

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SHORT COMMUNICATION

Bryoporus rugipennis Pandellé (Coleoptera: Staphylinidae) in Northern England.—

This rare montane beetle is mostly known from the north of Scotland, but it has also now been found at three English localities. Day (1923) mentions a record by Donisthorpe from Skiddaw, and K. Houston collected four females in pitfall traps at Cow Green, Upper Teesdale, County Durham in 1967 and 1968. The site is now under the reservoir. These four were identified for Houston by R. C. W. in 1974, but the record has never been published. Two were found in “*Calluna* grassland on glacial drift overlying Melmerby Limestone” (NY814303), the other two in *Festuca ovina* L. grassland (NY814303). The traps were in operation from late May to late July.

More recently, a single specimen was found by K. N. A. A. in an area of blanket peat bog at 670 m on the summit ridge about Scar Craggs (NY207206), to the west of Causey Pike in the Derwent Fells, Cumbria, 29.vii.1992. The vegetation here is of a typical undegraded high level blanket bog type, with a good cover of the dwarf shrubs *Calluna vulgaris* (L.) Hull, *Vaccinium myrtillus* L., and *Empetrum nigrum* L., plus some *V. vitis-idaea* L., within a matrix of *Eriophorum* and *Juncus squarrosus* L.

The information gathered for the forthcoming *Review of the scarce and threatened Coleoptera of Great Britain, Part 2* (Mark Parsons, pers. comm.) so far includes recent Scottish records only from Mid-Perth, S. Aberdeen, Easternness and Wester Ross vice-counties, with older records additionally from Stirlingshire and Elgin. Another unpublished record known to R. C. W. is of three taken in water traps by David Horsfield on 11.vii.1982, at Meall a'Chrsgaith (NH186734) Fannich Hills SSSI, Wester Ross. The traps were placed on “rocky *Racomitrium* heath” at 883 m altitude. It is also worth noting that R. C. W. never came across *B. rugipennis* himself during several years of intensive collecting in the Cairngorms and sorties to many other Scottish peaks. R. C. W. also identified all the Staphylinidae collected by R. Goodier in Snowdonia and no specimens of *B. rugipennis* were discovered.

K. N. A. A. would like to thank John Owen for his identification of the specimen of *B. rugipennis* and Mark Parsons for access to the as yet unpublished national review.—Keith N. A. Alexander, National Trust, 33 Sheep Street, Cirencester, Gloucestershire GL7 1QW, and R. C. Welch, Institute of Terrestrial Ecology, Monks Wood, Abbots Ripton, Huntingdon, PE17 2LS.

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